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A new genus and species of hermit crab (Crustacea, Anomura, Diogenidae) from the Timor Sea, north Australia

by Gary J. MORGAN and Jacques FOREST

Abstract. — A new genus and species of diogenid, *Tisea grandis*, is described from the Timor Sea. It is a very large species, probably the largest marine hermit crab. It is most similar to the genera *Dardanus* and *Petrochirus* but is distinguished by a combination of characters pertaining to the pattern of lineae and sulci on the carapace, the morphology of the chelipeds and the twisting of the dactyl of second and third pereiopods.

Résumé. — *Tisea grandis*, nouveau genre et nouvelle espèce de pagure Diogenidae, est décrit de la mer de Timor. C'est une espèce de grande taille, sans doute le plus grand des pagures marins. *Tisea* peut être rapproché des genres *Dardanus* et *Petrochirus*, mais il s'en distingue par une combinaison de caractères portant sur l'arrangement des lignes et sillons de la carapace, sur la morphologie des chélipèdes et sur la torsion des dactyles des deuxièmes et troisièmes péréiopodes.

G. J. MORGAN, *Department of Aquatic Invertebrates, Western Australian Museum, Francis Street, Perth, W.A. 6000, Australia.*
J. FOREST, *Laboratoire de Zoologie (Arthropodes), Muséum national d'Histoire naturelle, 61, rue Buffon, 75231 Paris cedex 05, France.*

Two very large specimens of an unusual hermit crab (fig. 1) were forwarded to one of us (GJM) by Dr A. J. BRUCE of the Northern Territory Museum, Darwin. These proved to be representatives of a new species that could not be assigned to any described genus of hermit crabs. The species has the bases of the third maxillipeds contiguous and is therefore assignable to the Diogenidae. It displays certain characters, however, that are unique amongst both the Diogenidae and Paguridae.

Type specimens are lodged in the Northern Territory Museum, Darwin (NTM) and the Muséum national d'Histoire naturelle (MNHN).

TISEA gen. nov.

DIAGNOSIS

Diogenid with carapace well calcified ; posterior carapace much inflated, bearing corneous-tipped spines dorsally and laterally. Cardiac sulci in close proximity for most of their lengths, fusing as single median sulcus anterior to posterior border of carapace. Sulci cardiobranchialis extending full length of carapace, converging on median sulcus at posterior

margin of carapace. Dorsolateral and lateral surface of carapace with numerous longitudinal and transverse lineae resulting in reticulated appearance. Linea anomurica difficult to distinguish from other lineae but appearing to extend full length of carapace at its longest point. Cervical groove distinct anteriorly but obsolete for most of length. Shield lacking Y-shaped linea delimiting posterior of mesogastric region.

Ocular peduncles short. Ocular acicles subtriangular, spinose.

Mandibles strong and massive, with well developed palp. Endopodite of maxillules lacking accessory flagellum. Maxillae with scaphognathite very well developed, with both proximal and distal lobes large, latter clearly extending beyond endopodite and slightly beyond distal endite. First maxillipeds with flagellum of exopodite biarticulate and epipodite long and subtriangular. Third maxillipeds with well developed crista dentata and contiguous basally.

Chelipeds and pereiopods 2-4 very spinose. Chelipeds subequal; chela fingers moving in oblique plane; finger tips corneous on both chelae. No stridulatory ridges. Dactyl of pereiopods 2 and 3 twisted so dorsal margin assumes lateral axis distally. Pereiopod 4 subchelate; pereiopod 5 chelate.

14 pairs of phyllobranchiae (including 1 pair of pleurobranchiae above pereiopod 5).

Abdomen large and coiled dextrally; tergites 2-4 well calcified, tergite 6 divided by deep transverse groove. Uropods small, asymmetrical, left larger than right. Brooding pouch absent on female.

Female with 4 unpaired pleopods; pleopods 1-3 very large, triramous, endopodite rami recurved (especially distal ramus), exopodite very elongate and somewhat curved; pleopod 4 tiny, biramous, exopodite 3-segmented and far exceeding minute endopodite. Male condition unknown.

Telson with median groove and shallow midlateral constrictions delimiting left and right posterior lobes, left larger than right.

Monotypic.

TYPE SPECIES : *Tisea grandis* sp. nov.

ETYMOLOGY : Named from a combination of letters after the type locality of the Timor Sea. Gender (attributed) : masculine.

Tisea grandis sp. nov.

(Figs 1-18, 21, 22)

MATERIAL EXAMINED : Holotype, ♀, shield length 58.8 mm, carapace length (midline) 127.6 mm, Timor Sea (9°43′ S, 130°00′ E to 9°47′ S, 130°25′ E), dredged 265-275 m, 9 December 1989-4 January 1990, NTM Cr.007119. — Paratype, ♀, shield length 54.0 mm, carapace length 121.5 mm, data as for holotype, MNHN Pg 4855.

DESCRIPTION

Shield (fig. 2) slightly longer than broad. Rostrum short and triangular, apex rounded, projecting as far as lateral projections. Lateral projections triangular, tipped by 2-3 minute but sharp spinules. Shield front concave between lateral projections and rostrum, slightly sinuous

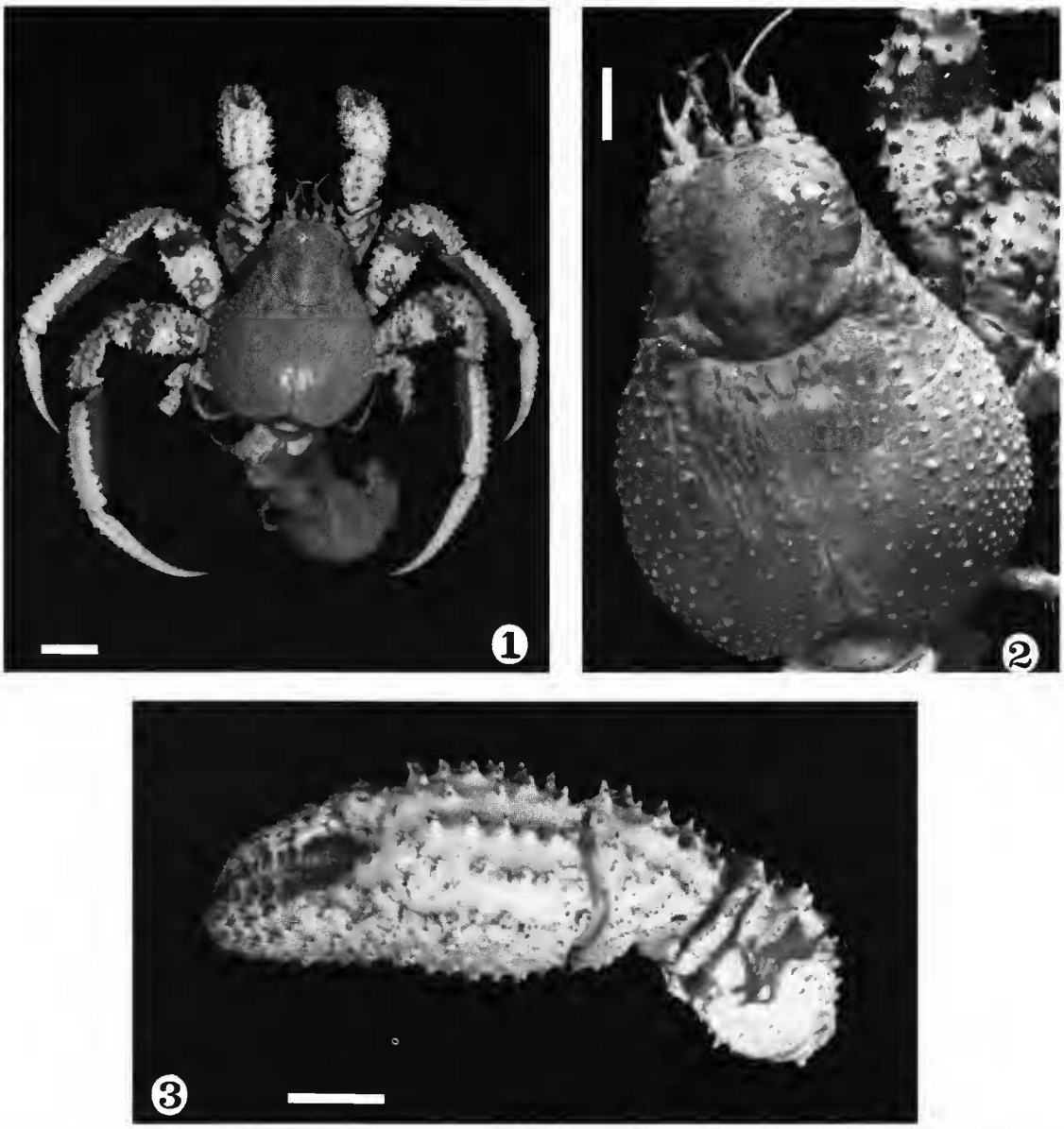
between lateral projections and anterolateral angles. Anterolateral and lateral margins with numerous corneous-tipped spines and spinules, these often in groups of 2-5; dorsal surface also with scattered corneous-tipped spines, some in short rows. Pattern of lineae as per genus.

Posterior carapace (fig. 2) much inflated, twice as broad as shield. Dorsolateral and lateral surfaces bearing numerous sharp corneous-tipped spines, these often in short rows of 3-4; spines largest laterally, decreasing in size and number dorsally. Cardiac sulci (figs 21, 22) converging after separation from linea transversalis and delimiting a nearly equilateral triangle, lateral borders of which slightly convex; surface of triangle bearing 5-8 small corneous-tipped spines arranged subsymmetrically. Cardiac sulci extending posteriorly from triangle, in close proximity to each other, separated by very narrow strip of cuticle, this strip separated from anterior triangle by short transverse sulcus; anterior triangle and median strip corresponding with posteromedian plate of PILGRIM (1973). Posterior to triangle, posteromedian plate narrow and regular until approximately 1/3 postcervical length, there widening slightly and bearing 2 protuberances, these centrally depressed and with a central pore. Posterior to protuberances, posteromedian plate very narrow, with small pored protuberance, similar to but smaller than those anterior, at approximate midlength of postcervical carapace. Cardiac sulci diverging somewhat posterior to this, with several short transverse or slightly oblique lineae dividing posteromedian plate of paratype, these lineae less developed in holotype. Cardiac sulci fusing as single median sulcus at approximately 1/3 of postcervical length from posterior margin of carapace in holotype, about 1/6 postcervical length from posterior margin in paratype; median sulcus continuing to posterior margin of carapace. Setation extremely light on carapace, with only scattered minute simple setae.

Diameter of corneas approximately 1/2 length of ocular peduncles. Peduncles short, less than 1/2 breadth of front of shield and less than 1/3 length of shield; peduncles distinctly expanded distally and proximally and bearing scattered small sharp corneous spines on dorsal surface, these mostly associated in pairs; some short simple setae. Ocular acicles broad basally, tapering distally; distal margin with 5-7 corneous-tipped spines and 1 additional proximodorsal spine.

Antennular peduncles long and slender, twice length of ocular peduncles; ultimate segment unarmed or with 1-2 distodorsal spines; penultimate segment with 1 distodorsal spine and 1 smaller spine posterior to this, and 1 minute distolateral spinule; basal segment with several distolateral and 2-3 strong distoventral spines.

Antennal peduncles longer than antennular peduncles by about 1/3 length of fifth segment of former; fifth segment with several small corneous spines in irregular dorsolateral and dorsomesial rows; fourth with 3-6 distodorsal corneous spines of varying sizes, irregular row of 5-8 corneous spines on lateral surface extending to distoventral angle and 2-3 distomesial spines; third with 7-8 strong corneous spines in row extending from lateral surface distoventrally slightly onto mesial face; second with numerous corneous spines, congregated in cluster of about 8 distolaterally and scattered dorsally and mesially; first segment with several small lateral spines and strong ventromesial process. Antennal acicles long, reaching beyond 1/2 length of fifth peduncular segment, tapering from broad base to point at apex; bearing numerous (35-40) corneous spines on dorsal, dorsomesial and lateral surfaces. Peduncular segments with scattered simple setae, these longest and densest ventrally on third segment. Antennal flagella (broken but retained) longer than cephalothorax, very weakly setose with minute simple setae.

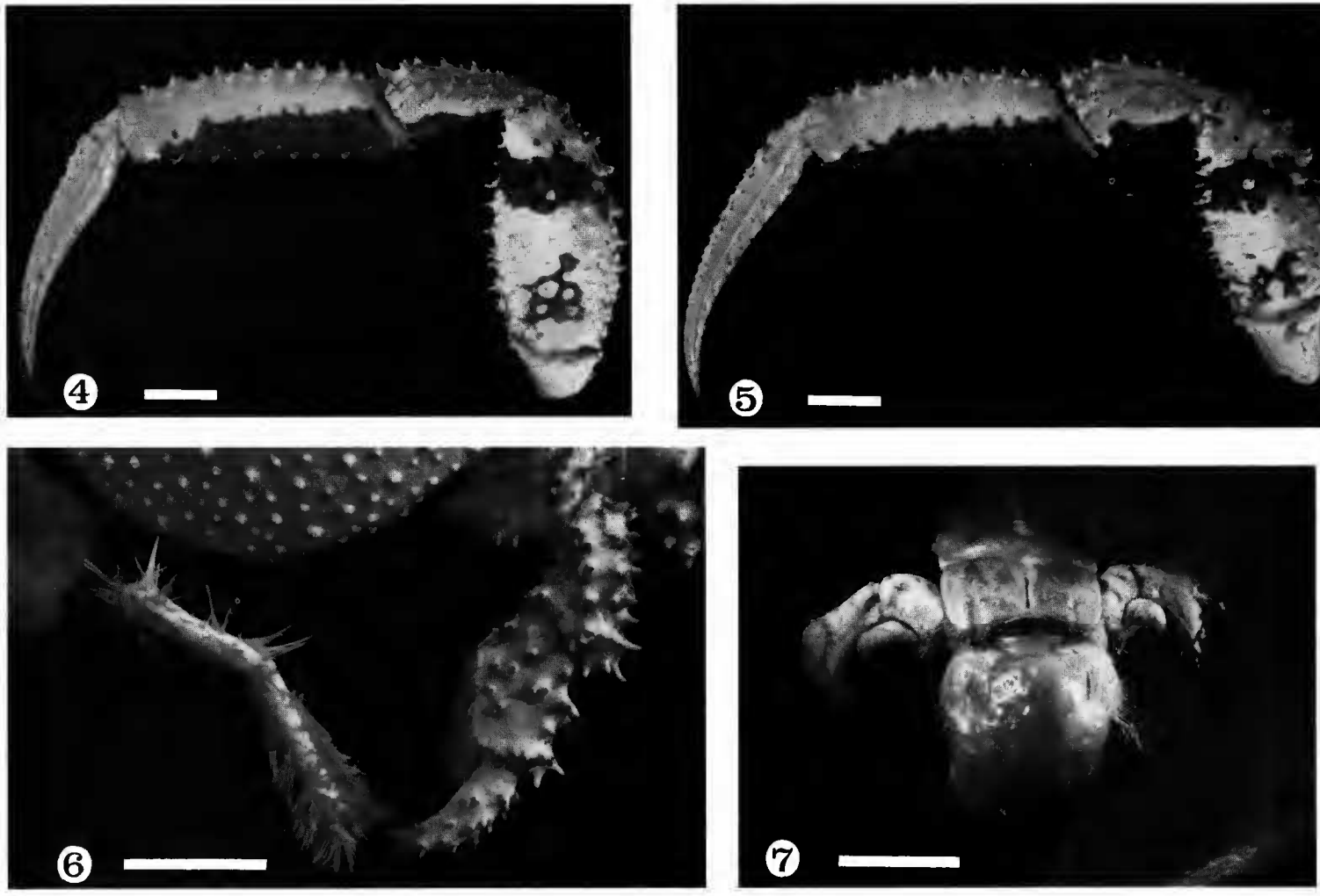


FIGS 1-3. — *Tisea grandis* gen. et sp. nov., holotype. 1, whole animal, dorsal view; 2, shield and posterior carapace, dorsal view; 3, left cheliped, lateral view. Scales = 40.0 mm (1); 20.0 mm (2, 3).

Mandible (fig. 8) with palp of 3 segments, tufts of setae on mesial lobe of second segment. Maxillule (fig. 9) with proximal endite subquadrate, distodorsal angle rather produced; endopodite lacking accessory flagellum (= external lobe), with several distal setae. Maxilla (fig. 10) with endopodite inflated basally and shorter than distal extension of scaphognathite. First maxilliped (fig. 11) with elongate endopodite, as long as basal segment of exopodite; flagellum of exopodite slightly longer than basal segment; epipodite well developed. Second maxilliped (fig. 12) with basis-ischium fusion nearly complete. Third maxilliped (fig. 13) with merus bearing 2 strong ventral spines and sometimes small distolateral spinule; basis-ischium fusion incomplete, ischium with well developed crista dentata of 11-12 teeth, no accessory teeth, 1 ventral spine on distal margin; basis with 1-2 small mesial spines; coxa with 3 spines at ventromesial angle.

Chelipeds (fig. 3) subequal, left (propodal length 83.7 mm) slightly larger than right (PL 80.5 mm) on holotype, right (PL 82.4 mm) slightly larger than left (PL 76.3 mm) on paratype; held with fingers moving obliquely. Dactyl slightly longer than 1/2 length of propodus, distinctly curved mesially; dorsal and lateral surfaces bearing numerous corneous-tipped spines, these largest proximolaterally; 2 very large flattened cutting teeth, distal 1/3 of gape corneous; mesial face smooth. Propodus slightly more than twice as long as broad; fixed finger similar to but overreaching dactyl, deflexed slightly and distinctly curved mesially; 2 very large flattened cutting teeth and 2 smaller teeth proximal to these; palm about as long as broad; palm and fixed finger bearing large sharp corneous-tipped spines on dorsal, lateral and ventral surfaces, spines in uneven rows on palm, less distinctly so on finger; many spines fused at bases in pairs; mesial face of propodus with more scattered, smaller spines. Carpus about as long as palm and similarly armed with corneous-tipped spines, these clustered in groups of 2-4. Merus longer than carpus; distal margin with numerous variously sized corneous-tipped spines; dorsal margin with series of transverse rows of corneous-tipped spines, these rows also on lateral face but comprising much smaller spines; ventrolateral and ventromesial edges with numerous spines, these mostly grouped in short rows. All segments with scattered tufts of simple setae, mostly emanating from bases of spines, setae heaviest on fingers.

Second pereiopods (fig. 4) much longer than chelipeds. Dactyl as long as propodus, lanceolate, tapering from broad base to narrow tip with sharp corneous claw and twisting distally (see generic diagnosis); dorsal margin with strong corneous-tipped spines, largely in clusters of 2-3 proximally, becoming smaller and contiguous distally where dorsal margin twists laterally; lateral face with distinct median sulcus, this deepest and broadest proximally; irregular row of corneous-tipped spines dorsal and immediately ventral to sulcus, these spines often in clusters of 2-3, largest proximally and very small distally; ventral margin with clusters of strong spines on proximal 1/3, spines small or absent distal to this; mesial face similar to lateral face proximally, including median sulcus, but distal 1/2 with 1 short (immediately proximal to claw) and 3 long oblique sinuous ridges of corneous spines extending from dorsal to ventral margins, and 2 much shorter ridges of spines posterior to these; setae in sparse tufts over most of dactyl but crests of long setae along distodorsal margin twisting laterally and along oblique ridges on distomesial face. Propodus distinctly compressed laterally; dorsal and ventral margins with clusters of 2-3 strong corneous-tipped spines, lateral and mesial faces with spaced clusters of much smaller spines. Carpus about 2/3 length of propodus, dorsal and lateral faces with strong corneous-tipped spines, these mostly in clusters of 2-3 and largest dorsally; spines much smaller mesially and ventrally. Merus approximately same length as



FIGS 4-7. — *Tisea grandis*, holotype. 4, left second pereiopod, lateral view; 5, left third pereiopod, lateral view; 6, right fourth and fifth pereiopod, lateral view; 7, tailfan, dorsal view. Scales = 20.0 mm (4-6); 10.0 mm (7).

propodus, compressed laterally; dorsal margin with transverse rows of corneous-tipped spines similar to merus of chelipeds; lateral face with short rows of much smaller spines; ventral margin with numerous large irregularly clustered spines; mesial face almost smooth. Propodus, carpus and merus very sparsely setose, with scattered tufts of short simple setae.

Third pereiopods (fig. 5) slightly longer than second due primarily to longer dactyl and ischium. Ornamentation and setation similar to second except spines larger on lateral face of merus. Female with paired coxal gonopores. Sternite of third pereiopods strongly produced, subovate, on paratype bearing 2 sharp spines anteriorly.

Fourth pereiopods (fig. 6) subchelate, with well developed propodal rasp extending more than 1/2 ventral length of propodus; all segments with strong corneous-tipped spines dorsally and laterally.

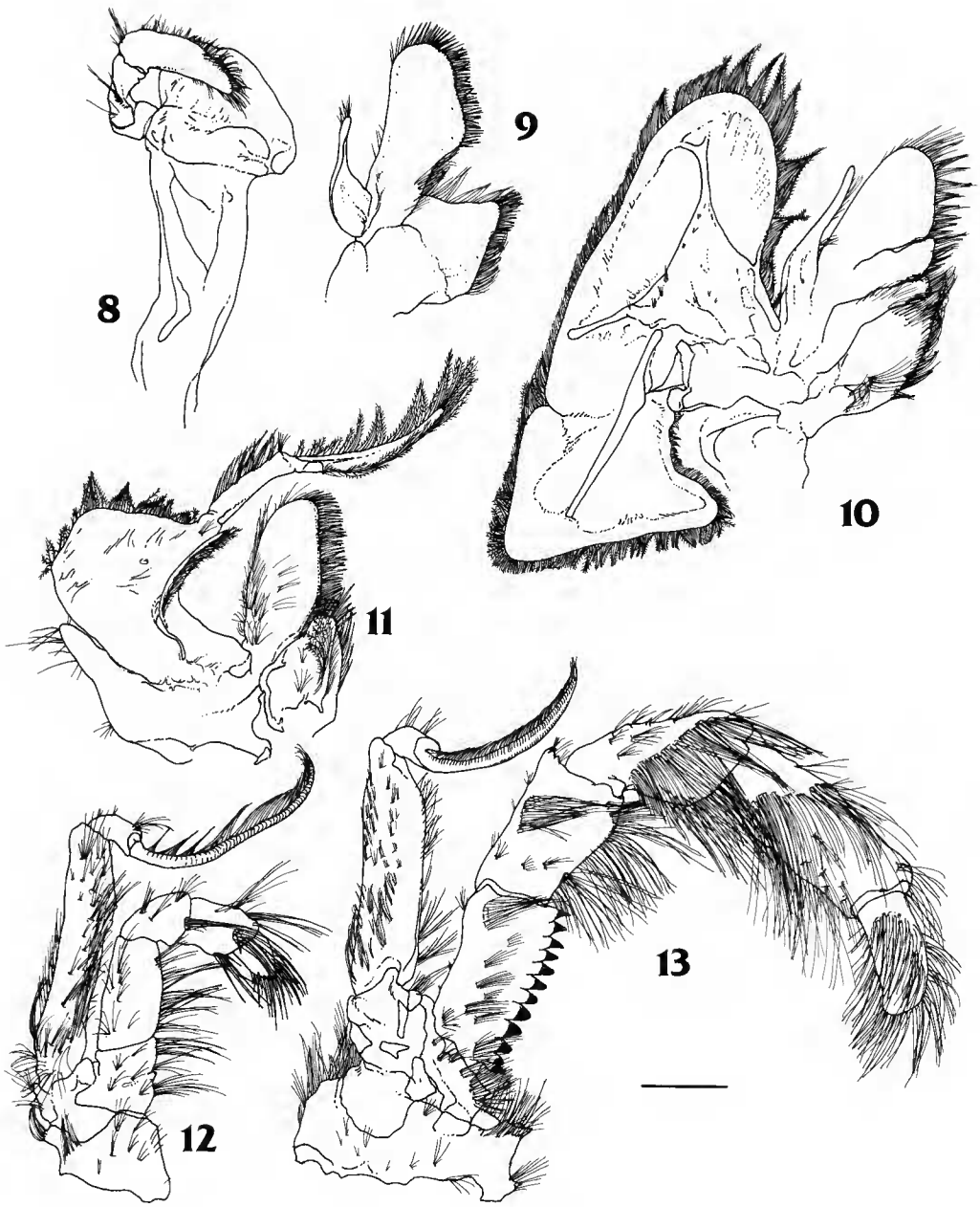
Fifth pereiopods (fig. 6) chelate, unarmed, with dense tufts of long simple setae on all segments.

Abdomen with tergites 2-4 large, slightly decreasing in size posteriorly, strongly calcified especially on left side where pleopods insert on thick, smooth, rather lustreous plate, separated from remainder of tergite by fine sulcus. Tergite 1 small, more lightly calcified. Tergite 5 widely separated from preceding tergite, much smaller and chitinous.

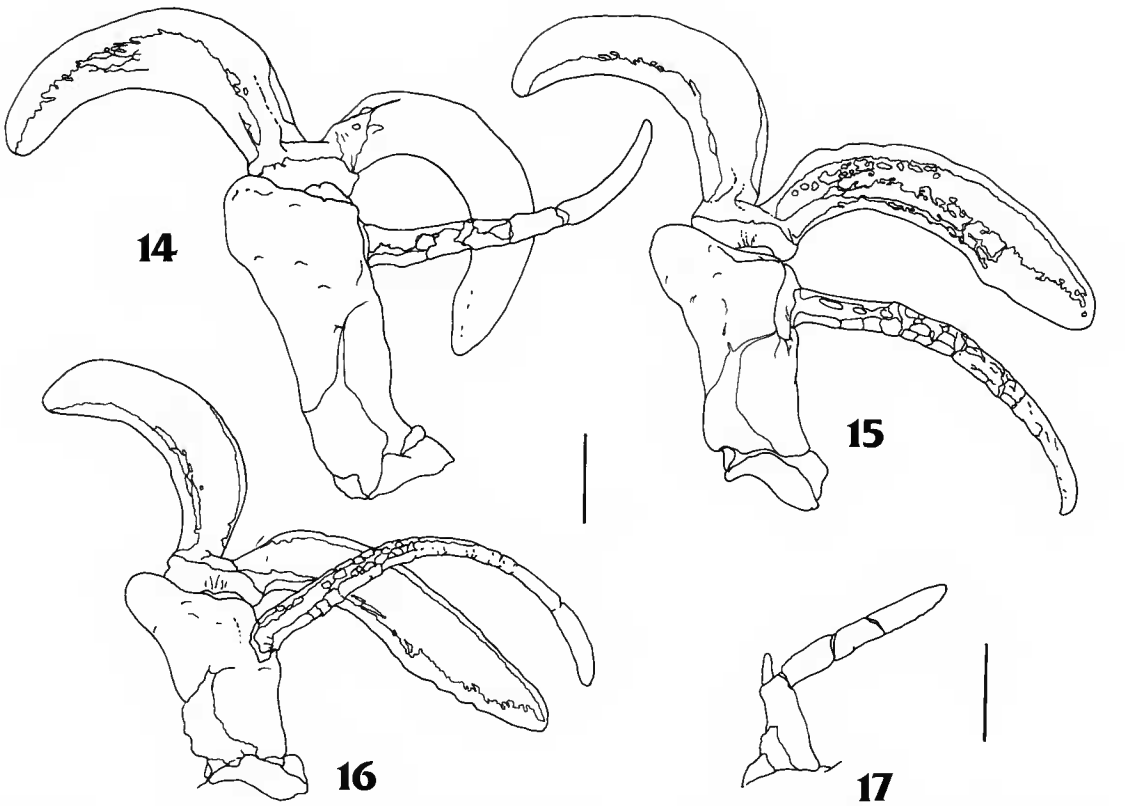
Female with 4 unpaired pleopods. Anterior 3 pleopods very large and triramous (pleopods damaged and lacking complete rami on holotype). First pleopod (fig. 14) with long protopodite, weakly inflated distally; 2 subequal endopodite rami, both strongly recurved and lacking any trace of segmentation; exopodite similar length to these but very elongate and showing traces of segmentation. Second pleopod (fig. 15) with shorter protopodite, strongly inflated distally; distal ramus of endopodite similar size and shape to that of first pleopod, lateral ramus more elongate and less strongly curved; exopodite slightly longer than on first pleopod. Third pleopod (fig. 16) with short protopodite, strongly inflated distally; distal ramus of endopodite shorter than on first and second pleopods, lateral ramus even less curved than on second; exopodite slightly longer and thinner than on second pleopod. Last pleopod (fig. 17) minute and biramous with exopodite 3-segmented and much larger than 1-segmented endopodite (pleopod 4 missing on paratype).

Tailfan (fig. 7) asymmetrical, left uropod larger than right; uropods small, shorter than tergite 6. Sixth abdominal tergite unarmed except for several minute spinules on posterior margin. Telson with median cleft, left posterior lobe slightly larger than right, both broadly triangular; telson lacking spines but fringed with long and short simple setae.

Coloration (preserved specimens) : Shield with irregular, subsymmetrical mottling of dark red on pink-orange, with cream areas anterolaterally. Posterior carapace mostly pink with some areas of red, spines cream. Ocular peduncles cream proximally, deep red for distal 1/2, with cream at base of corneas; ocular acicles cream with red area proximally. Antennular peduncles cream with red mottling dorsally on ultimate segment. Antennal peduncles cream with red patches especially proximally on second segment and laterally on acicle, fifth segment pale pink-orange with darker red dorsally and ventrally; flagella pink-orange. Chelipeds predominantly cream; propodus with small arca of red proximoventrally; carpus with red ventrally, small red patches dorsally and pink area proximally; merus with large irregular area of red distally. Second and third pereiopods with dactyl cream with some small patches of red near mesial ridges; propodus predominantly cream with pink tinge dorsolaterally, ventral 1/2



FIGS 8-13. — *Tisae grandis*, holotype, left mouthparts, internal view. 8, mandible; 9, maxillule; 10, maxilla; 11, first maxilliped; 12, second maxilliped; 13, third maxilliped (exopodite retracted slightly from endopodite for clarity). Scale = 6.0 mm.



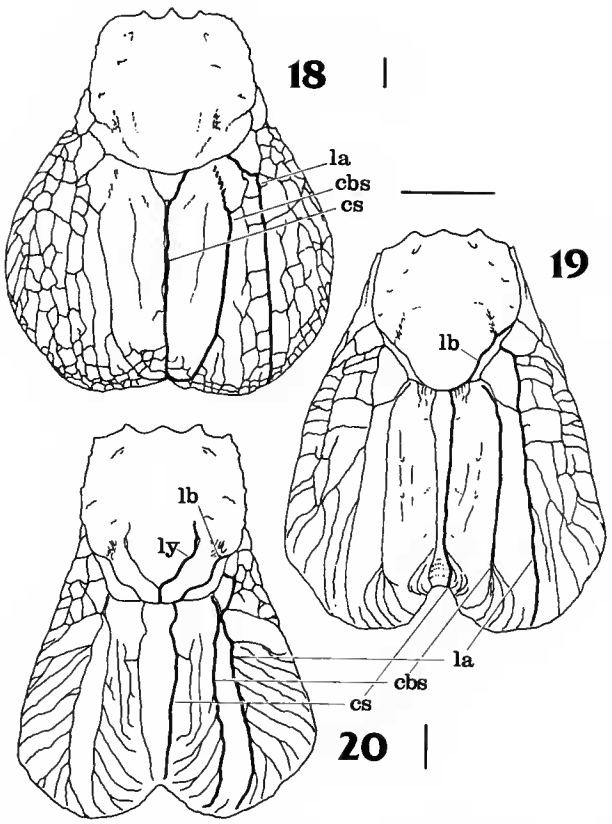
FIGS 14-17. — *Tisea grandis*, female pleopods, dorsal view, setae omitted. 14-16, paratype; 17, holotype. Scales = 6.0 mm (14-16); 2.0 mm (17).

of lateral face and ventral margin deep red, this extending slightly onto ventromesial face; carpus cream with pink tinge, large area of deep red ventrally and small red patches dorsally; merus cream with pink tinge dorsally, deep red subdistal band on lateral surface, this extending onto ventral and dorsomesial faces, also red patches on some clusters of spines dorsally and large red patch proximolaterally. Fourth and fifth pereiopods cream, fourth with some small patches of red. Tailfan cream-brown.

ETYMOLOGY : Named from the latin for 'large'.

DISTRIBUTION : Known only from the type locality.

HABITAT : 265-275 m depth. Apparently inhabiting gastropod shells but species unknown. Probably living with cephalothorax protruding from the shell (see Discussion).

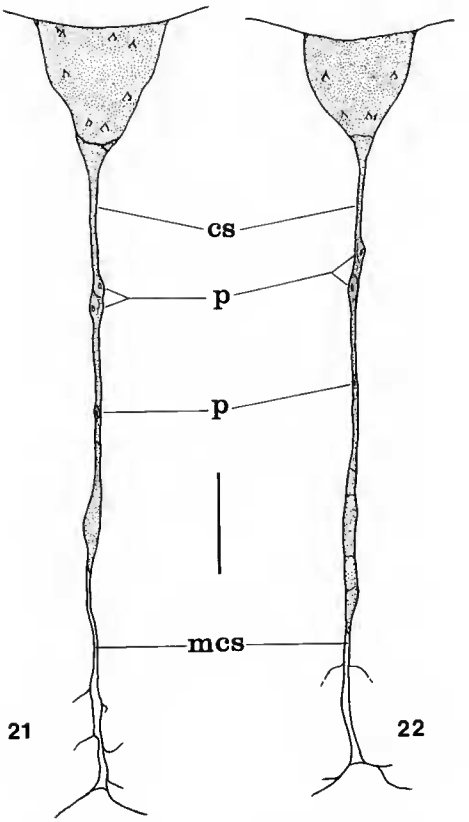


FIGS 18-20. — Shield and posterior carapace lineae and sulci noted in text. 18, *Tisea grandis*; 19, *Petrochirus pustulatus*; 20, *Dardanus megistos*. cs, cardiac sulcus; cbs, sulcus cardiobranchialis; la, linea anomurica; lb, linea 'b' = cervical groove; ly, 'Y' linea. Scales = 10.0 mm.

DISCUSSION

Tisea grandis is an extraordinarily large hermit crab, comfortably exceeding in size the largest species of *Dardanus* (e.g. *D. megistos* (Herbst), *D. brachyops* Forest, *D. australis* Forest and Morgan : see FOREST, 1962; FOREST and MORGAN, 1991). *Petrochirus pustulatus* (H. Milne Edwards) has been reported at a size of 110 mm total carapace length (FOREST, 1966 : 148). This would correspond to approximately 100 mm median carapace length and 45 mm shield length, again considerably smaller than *T. grandis*. The very recent discovery of such a large species must be attributable to the considerable depth at which *T. grandis* occurs.

The genus *Tisea* most closely resembles *Dardanus* and *Petrochirus*. The chelipeds are subequal in size and form, a rare trait for *Dardanus* but usual for *Petrochirus*. In the latter, the right cheliped is consistently slightly larger than the left while in *Tisea*, either chela may slightly exceed the other. In addition, in *Petrochirus* at least the right chela lacks corneous tips



FIGS 21-22. — *Tisea grandis*, cardiac sulci and posteromedian plate (stippled). 21, holotype; 22, paratype. cs, cardiac sulci; mcs, median cardiac sulcus; p, median pored protuberances. Scale = 10.0 mm.

to the fingers while in the new genus both chelae have corneous finger tips as in *Dardanus*. The dactyls of second and third pereiopods are notably twisted in *Tisea*, as in *Petrochirus* but not in *Dardanus*.

The mouthparts of the three genera are very similar. The distal lobe of the scaphognathite and the epipodite of the first maxilliped are longer in *Tisea* than in *Petrochirus* and *Dardanus*.

The female pleopods of *Tisea* resemble those of *Dardanus* and *Petrochirus* in general morphology (see FOREST, 1984, figs 24-27). In *Tisea* the distal ramus of the endopodite is more strongly recurved than in *Dardanus* and much more strongly than in *Petrochirus*. The lateral ramus of the endopodite is also more curved than in *Petrochirus*. The exopodite most closely resembles that of *Petrochirus*, however, being very elongate, but differs in being distinctly curved.

The strong calcification of, and numerous spine-tipped tubercles on, the posterior carapace are unusual in marine hermit crabs. The pagurid genus *Labidochirus*, containing two species, shows similar characters (see MCLAUGHLIN, 1974, figs 92, 95; MIYAKE, 1982, pl. 41, fig. 1). In *Labidochirus* this condition is related to the ecology of the two species, where the

animals have only the abdomen lodged in a protective gastropod shell and the anterior of the body is exposed (MAKAROV, 1938 : 196). One might assume that *Tisea grandis* exhibits similar behaviour, if only because it is most unlikely that the animal could find a gastropod shell sufficiently large to accommodate the entire body.

In the pattern of lineae and sulci on the carapace, the genus *Tisea* appears to be unique amongst not only diogenids but also pagurids. Before this can be discussed, however, we must note some confusion in the literature regarding the nomenclature of carapace lineation in hermit crabs.

BOAS (1926 : 24, fig. 16) illustrated and named several cephalothoracic lines and sulci including the sulcus cardiobranchialis (BOAS, fig. 16, letter a). This feature corresponds with the branchiocardiac groove of PILGRIM (1973 : 367, fig. 1, letters bc). MCLAUGHLIN (1974 : 10, fig. 2) designated this sulcus as sulcus a′ but used the term sulcus cardiobranchialis for a feature illustrated, but unnamed, by both BOAS (1926) and PILGRIM (1983), namely the lines laterally delineating the postero-median plate of PILGRIM (1973). We see no reason to deviate from the original designation and therefore employ the term sulcus cardiobranchialis *sensu* BOAS (1926) rather than *sensu* MCLAUGHLIN (1974). All of the above workers agree in their designation of the linea anomurica.

The sulci laterally bordering the posteromedian plate remain unnamed. Because of their importance in comparative studies of hermit crabs, we believe it to be desirable to assign them a name and in this work have designated them the "cardiac sulci". We do so without implication of homology with structures in other non-hermit anomuran or non-anomuran decapod taxa.

These sulci display some notable variation in their conformation and position in the Coenobitoidea and Paguroidea but their configuration is relatively constant within genera. In all coenobitoids and paguroids except *Tisea*, the cardiac sulci, when they exist, are clearly separated for their entire length, although in *Birgus latro* (Linnaeus) they intersect at one point forming an hourglass pattern. In *Tisea*, the sulci converge and then continue posteriorly in very close proximity (on first inspection appearing to be fused) and in fact fusing for the posterior 1/6 to 1/3 of the postcervical carapace (figs 18, 21, 22). In the Diogenidae, only the genus *Petrochirus* approaches this condition with cardiac sulci in relatively close proximity and the posteromedian plate very narrow (fig. 19). No anterior triangle is present in *Petrochirus* however and the two cardiac sulci are still clearly distinct and separated.

In addition, in *Tisea* the sulci cardiobranchialis extend the full length of the carapace. This latter condition is approached by *Petrochirus* and *Dardanus* species, where the sulci diverge in a dendritic pattern to the posterior margin of the carapace (figs 19, 20). The linea anomurica extends to or almost to the posterior carapace margin in several other genera including *Petrochirus* and *Dardanus*.

Like *Petrochirus, Tisea* lacks the Y-shaped pattern of lines posteriorly delineating the mesogastric region, so evident in *Dardanus* (fig. 20). In *Tisea*, the cervical groove (line "b" of BOAS (1926) and MCLAUGHLIN (1974)) is very shallow and poorly defined except anteriorly. The cervical groove is distinct in both *Petrochirus* and *Dardanus* (figs 19, 20).

The close proximity of the third maxillipeds and the structure of other characters confirm *Tisea* as a member of the Diogenidae. *Tisea* shows close affinities with a group of genera characterised by the possession of 14 pairs of branchiae and of unpaired triramous pleopods 2-4 on the female, and by the absence of an accessory flagellum on the endopodite of the

maxillule. This group comprises, on the one hand, *Aniculus* and, on the other, *Dardanus* and *Petrochirus*. *Aniculus* displays a number of characters that isolate it from the latter two genera (FOREST, 1984 : 17) and from *Tisea*. It is possible, however, that the transverse cardiac sulcus of *Aniculus* (and some *Dardanus*) is homologous with the short transverse sulcus posteriorly bordering the anterior triangle on the carapace of *Tisea*. *Tisea* shows close affinities with *Dardanus* and *Petrochirus*, particularly evident in the structure of the buccal appendages and of the pleopods of females. These similarities are unlikely to have resulted from convergence. The pattern of sulci and lineae on the carapace of *Tisea* shows closest similarity to that of *Petrochirus* It seems probable that *Tisea, Petrochirus* and *Dardanus* share a common, if distant, ancestor.

Tisea has attained a very large size and, as discussed earlier, in life probably has only the abdomen totally concealed within a protective gastropod shell. The strong calcification and spination of the posterior carapace can be interpreted as adaptations to this mode of life. The adaptative advantage, if any, of the convergent cardiac sulci is unknown but may also be related to lifestyle.

Dardanus is an extremely widespread genus but *Petrochirus* is restricted to the west and east Atlantic and east Pacific. The type locality of *T. grandis* would suggest then a long period of isolation from *Petrochirus*. Similarly, while *Dardanus* inhabits a wide bathymetric range. *Petrochirus* is confined to shallow waters, usually 20-60 m, and *Tisea* is known only from depths greater than 250 m.

It is an interesting coincidence that the "living fossil" glypheid, *Neoglyphea inopinata* Forest and De Saint Laurent, was collected in 1987-88 from the Timor Sea at 9°46′ S, 130°00′ E, at depths of 240-265 m (BRUCE, 1988 ; FOREST, 1989). It is noteworthy that two such remarkable species should be found at the same locality but the biogeographic significance of this is uncertain.

Acknowledgements

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